

STUDIES IN AUSTRALIAN *NEUROPTERA*.NO. 5. THE STRUCTURE OF THE CUBITUS IN THE WINGS OF THE
MYRMELEONTIDÆ.

BY R. J. TILLYARD, M.A., D.Sc., F.L.S., F.E.S., LINNEAN
MACLEAY FELLOW OF THE SOCIETY IN ZOOLOGY.

(With three Text-figures).

In No.1 of this series of Studies,* I worked out the wing-venation of *Myrmeleon uniseriatus* Gerst., from the pupal wing-tracheation, and showed how, in the forewing, the apparently simple vein M was in reality a forked vein, the vein usually considered to be Cu_1 being in reality the *cubito-median*, $Cu_1 + M_2$, and the point of incidence of M_2 on to the line of Cu_1 being marked by the foot of the oblique vein O. The branch descending from the point of bifurcation, which I called the cubital fork (*cuf*), was, naturally enough, taken to be Cu_2 . It was on the lack of specialisation of this branch, that I based my argument for the recognition of the tribe *Protoplectrini*, of which the correct name should be *Creagrini*, as previously given by Navás.

In No.4 of this same series of Studies,† when describing the wing-venation of the *Hemerobiidæ*, I showed how, in the forewings of *Drepanopteryx* and *Drepanacra*, an archaic Cu_2 was present close to the base, and that, in addition to this, Cu_1 was strongly branched at a sharp angle, much further distad, into two veins which I called Cu_{1a} and Cu_{1b} . In the allied genus *Drepanomina*, the archaic Cu_2 is lost, and replaced by a furrow. In the majority of the smaller *Hemerobiidæ*, even the furrow has disappeared. Thus, in the most highly specialised forms of the family *Hemerobiidæ*, all traces of the original Cu_2 are lost, and

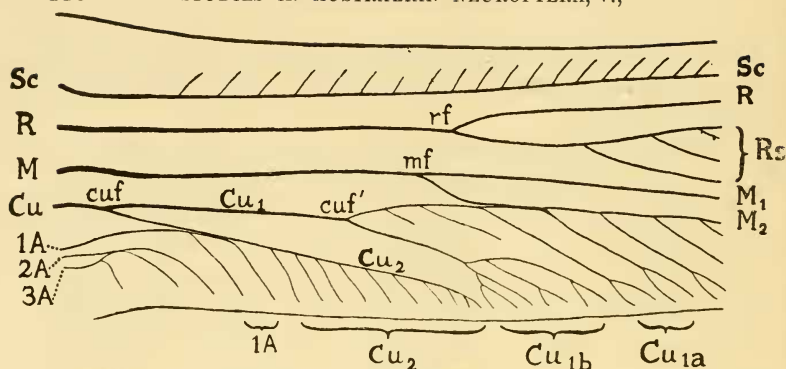
* These Proceedings, 1915, xl., Pt.4, pp.734-751, Pl. lviii.

† *Op. cit.*, 1916, xli., Pt.2, pp.269-332, Pls. xii.-xix.

there is left only the distal secondary forking of Cu_1 into Cu_{1a} and Cu_{1b} , the point of bifurcation being properly termed the *secondary cubital fork* (*cuf'*).

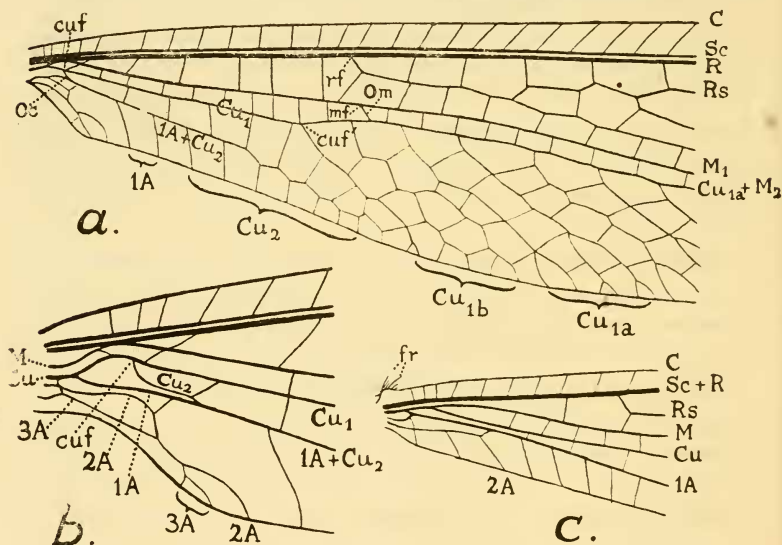
Now the resemblance between the condition of the cubitus in the forewings of these smaller specialised *Hemerobiidae*, and in the forewings of the *Myrmeleontidae*, is too striking to be ignored. It suggested to me at once that the veins which I had named Cu_1 and Cu_2 in the *Myrmeleontidae* were in reality only Cu_{1a} and Cu_{1b} respectively, and that, if the true Cu^2 still existed, it must be sought for near the extreme base of the wing. I therefore examined a considerable number of *Myrmeleontidae*, and found that, in many cases, there could be detected, close to the base of the wing, a semi-opaque connecting-vein, not unlike an oblique vein, (though not so well defined) running across from Cu_1 to 1A. This appeared to me to be the remains of Cu_2 . With a view to proving this point, I decided to examine the pupal tracheation of some of the older *Myrmeleontidae*, belonging to the subfamily *Dendroleontinae*, in the imagines of which this supposed remnant of Cu_2 appeared to be much more evident than in the genus *Myrmeleon* itself.

Most of the larvæ of the *Dendroleontinae* do not make pit-falls, but must be sought for either in loose sand, or in rubble or débris collected at the bases of large trees. During the winter of 1916, larvæ of several genera of this type were collected around Sydney. A number of these spun up in the following September. At the end of a fortnight, three likely-looking cocoons were opened, but were found still to contain larvæ. They were then placed under close observation until pupation took place. The first pupa examined proved to be very recently formed; so that, although a good dissection of the forewing was obtained, the structure was so exceedingly delicate that all the air passed out of the tracheæ before either a photomicrograph or a camera-lucida drawing could be obtained. With the second dissection, I decided to take no risks, but removed it at once to the microscope-stage, and made a camera-lucida drawing of it. Both the pupal tracheation and the imaginal venation showed up very clearly, and the result was



Text-fig. 1.

Tracheation of forewing in the pupa of *Xantholeon helmsi* Tillyard; ($\times 35$).



Text-fig. 2.

Venation of *Xantholeon helmsi* Tillyard; *a*, basal half of forewing, ($\times 4\frac{1}{2}$);

b, basal portion of same, enlarged, ($\times 10$); *c*, base of hindwing, ($\times 4\frac{1}{2}$).

LETTERING OF TEXT-FIGURES.

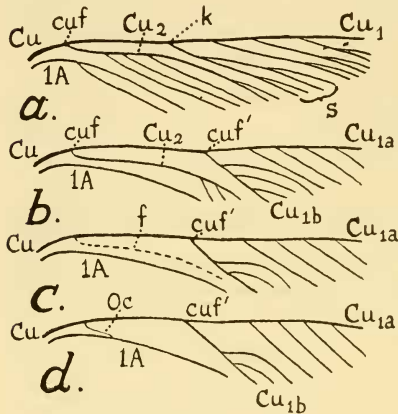
1A, 2A, 3A, first, second, and third analis, respectively—1A+Cu₂, cubito-anal—C, costa—Cu, cubitus; Cu₁, Cu₂, its two principal branches; Cu_{1a}, Cu_{1b}, the two principal branches of Cu₁—Cu_{1a}+M₂, cubito-medial—*cuf*, primary, and *cuf'*, secondary cubital fork—*fr*, vestigial frenulum—M, media; M₁, M₂, its two principal branches—*mf*, median fork—Oc, cubital oblique vein—Om, median oblique vein—R, radius—Rs, radial sector—*rf*, radial fork—Sc, subcosta.

a complete success, which is here reproduced in Text-fig.1. As the venation was complete, and even the delicate pigmentation of the imaginal wing could be noted, I was easily able to determine this wing as belonging to the rather rare insect *Xantholeon helmsi* Tillyard,—a result as fortunate as it was unexpected, since *Xantholeon* is certainly one of the most archaic of our Australian *Myrmeleontide*.

The result of this examination can be gathered by comparing Text-figs. 1 and 2. It will be seen that it not only bears out in full my suspicions concerning the real position of Cu_2 , but shows also a further unexpected point of interest. For the *trachea* Cu_2 is not a weak remnant descending to $1A$, as the examination of the imaginal venation had led me to suspect, but is a strong trachea which has captured the line of $1A$, in the same manner that M_2 has captured the line of Cu_{1a} . In both cases, it is the upper trachea that prevails, the lower that goes under. In both cases, the crossing of the upper trachea on to the level of the lower is marked, in the imaginal venation, by an *oblique vein*, which represents, of course, the actual basal piece of the upper vein in question. We must therefore distinguish in future between the *median oblique vein* (Om) and the *cubital oblique vein* (Oc). This latter is very clearly marked in *Xantholeon* (Text-fig.2), also in *Glenoleon*, *Acanthactisis*, and other genera; but it cannot be satisfactorily made out in our Australian species of the genus *Myrmeleon*, which are more highly specialised.

The process by which M_2 and Cu_2 have attained their present positions may be described as a process of "trachea-capture." The two tracheæ run at first more or less parallel. As the wing becomes narrower, they come to lie side by side. The oxygen-supply conveyed by both is now no longer fully needed; so that, in course of time, the weaker (in this case the lower) trachea becomes aborted, being reduced to a remnant impinging upon the strong upper trachea from below. In the resulting imaginal wing-venation, however, where the determining factor is not oxygen-supply, but the wing-stresses brought about during forward flight, the vein formed along the course of the lower trachea

continues the line of the stronger upper trachea beyond the point where the partially aborted lower trachea ceases to exist, and must, therefore, be regarded as a composite vein, whose double origin is now only indicated by the oblique vein placed above it. Thus, in the case under consideration, we have two composite veins formed, viz., the *cubito-median*, $Cu_{1a} + M_{2s}$ (whose structure I worked out in No.1 of this series of Studies), and the *cubito-anal*,



Text-fig.3.*

1A + Cu_{2s} , whose existence has not been before suspected. The oblique vein indicating the presence of the former is Om, that indicating the presence of the latter is Oc. The complete, correct, amended notation for the forewing of *Xantholeon helmsi* Tillyard, is given in Text-fig. 2. In Text-fig.3, I offer a phylogenetic series of stages to show the evolution of the Myrmeleontid

type from the original archaic formation of these veins, as still preserved for us in the archaic *Hemerobiidae*, *Drepanopteryx*, and *Drepanacra*.

* Phylogenetic series illustrating the evolution of the cubitus in the wings of *Hemerobiidae* and *Myrmeleontidae*.—Series a, b, c, three stages leading to the reduced Hemerobiid type, also to the type found in *hindwings* of *Nymphidae* and *Myrmeleontidae*. With a, compare forewing of *Drepanopteryx*; with b, compare hindwing of *Drepanopteryx*; with c, compare wings of *Drepanomina*. The final stage, in which the furrow f is completely eliminated, is not shown in this figure.—Series a, b, d, three stages leading to the formation of the cubito-anal vein in the *forewing* of the *Myrmeleontidae*, by fusion of the veins 1A and Cu_2 . In d, the basal part of Cu_2 is indicated by the cubital oblique vein Oc.

Lettering as on p.118, and, in addition, k, the point destined to become *cuf'*, and s, the sector of Cu_1 destined to become Cu_{1b} .

In Text-fig. 2, *c*, I have figured the base of the hindwing of *Xantholeon helmsi* Tillyard, in order to contrast the simplified condition of this wing with the complicated condition of the forewing discussed above. Since the *Myrmeleontidae* are admittedly derived from Nymphid-like ancestors; and since, in the *Nymphidae* themselves, both the media and the cubitus of the hindwing are already simple, unbranched veins, it must follow that this condition is to be found in their derivatives, the *Myrmeleontidae*. It should, however, be noted that there are signs of specialisation even in the hindwing, in that the vein 1A approaches basally very close to Cu, very nearly fusing with it; while Sc and R are completely fused together throughout the basal portion of the wing.

We have now to consider whether our new discoveries on the structure of the cubitus require us to make any revision in the present classification of the *Myrmeleontidae*. Esben-Petersen, in Part iii. of his "Australian Neuroptera,"* has named the area between $Cu_{1a} + M_2$, Cu_{1b} , and the hindmargin of the wing, the *intercubital area*, and has pointed out that a Banksian Line is sometimes developed in this space; such a line, he calls the *intercubital line*. With this I am in agreement. Now the development of an intercubital line is evidence of high specialisation in this area. Therefore, those genera in which it occurs, if they have hitherto been regarded as primitive, must have their position reconsidered. In the tribe *Creagrini*, this intercubital line is beautifully developed, and is correlated with a condition of parallelism between $Cu_{1a} + M_2$ and Cu_{1b} . It was natural, so long as this latter vein was taken to be Cu_2 , that this condition of parallelism should be considered primitive. But the archaic condition existing for Cu_{1b} is not one of parallelism to $Cu_{1a} + M_2$, but rather, as may be seen in *Xantholeon*, one of strong divergence from it, Cu_{1b} running obliquely to the margin, and parallel to the numerous branches descending from $Cu_{1a} + M_2$. *Xantholeon*, *Gymnocnemia*, *Periclystus*, and other genera show this

* These Proceedings, 1917, xlii., Pt. 1, pp. 203-219, Pl. x.-xv. (Pl. x., fig. 1, *Protoplectron striatellum* Esb.-Pet.).

primitive condition well. From this primitive state, two lines of development may follow:—

(1) Cu_{1b} may become fixed in its divergent position, and the intercubital line may be developed in the usual manner between the descending branches of $Cu_{1a} + M_2$. Various stages in this process may be studied within the genus *Glenoleon*, while the complete formation may be seen in *Acanthaclisis* and *Myrmeleon*.

(2) Cu_{1b} may become straightened out parallel to $Cu_{1a} + M_2$, the intercubital line becoming developed between them, and parallel to both. The beginning of this line of evolution is evident in the forewing of *Protoplectron striatellum* Esb.-Pet., which is, therefore, fairly primitive. In *P. venustum* Gerst., the formation is practically completed; while in *Creagris plumbeus* Ol., (Palearctic) the development of the three parallel veins, with all connecting structures reduced to simple series of cross-veins, reaches the highest possible stage of evolution along this line.

It would appear, therefore, that my estimate of the tribe *Creagrini*, as the most primitive of the *Dendroleontinae*, is not correct. They form, rather, a separate side-line of development away from the main stem, culminating in a very highly specialised genus, viz., *Creagris*. It should be noted, in this connection, that the larva of *Creagris* is the only one amongst the *Dendroleontinae* that is known to make pit-falls. It will now be of special interest to find out whether the larvæ of *Protoplectron* do likewise.